Sea buckthorn berries Hippophae rhamnoides L. predict size and composition of a great tit population Parus major L.

Tinbergen, J. M.; Fokkema, R. W.; Pen, I.; Ubels, R.

Published in:
Journal of Avian Biology

DOI:
10.1111/jav.02037

Publication date:
2019

JOURNAL OF
AVIAN BIOLOGY

Article

Sea buckthorn berries *Hippophae rhamnoides* L. predict size and composition of a great tit population *Parus major* L.

J. M. Tinbergen, R. W. Fokkema, I. Pen and R. Ubels

J. M. Tinbergen (https://orcid.org/0000-0003-4581-7164) ✉ (j.m.tinbergen@rug.nl), R. W. Fokkema, I. Pen and R. Ubels, Conservation Ecology Group, Groningen Inst. for Evolutionary Life Sciences (GELIFES), Univ. of Groningen, Groningen, the Netherlands. RWF also at: Evolutionary Biology, Bielefeld Univ., Bielefeld, Germany, and Dept of Animal Behaviour, Bielefeld Univ., Bielefeld, Germany.

Journal of Avian Biology
2019: e02037
doi: 10.1111/jav.02037

Subject Editor: Jan-Åke Nilsson
Editor-in-Chief: Thomas Alerstam
Accepted 13 July 2019

In seasonal environments variation in food abundance in the non-breeding season is thought to affect songbird population dynamics. In a unique tit-sea buckthorn berry system we can estimate the berry abundance and both the tit consumption and population dynamics. Six hundred nest boxes were available to great and blue tits *Cyanistes caeruleus* for breeding in spring and roosting in winter. We followed the dynamics including the recapture histories of individually marked great tits from 2008 to 2014. In each year we estimated 1) the winter sea buckthorn berry availability, 2) an index of berry consumption in December based on the colour of the faeces of roosting birds, 3) the number of breeding great and blue tits, 4) both recapture probability and the return rate of the great tits and 5) immigration rates. December berry abundance positively predicted the number of breeding pairs of both species in the subsequent season and great tit return rates in the second half of the winter. There was support for a sex specific berry effect on the adult return rate in the great tit: female return rate was associated less strongly to berry abundance than male return rate. This skewed the sex ratio of the local breeders in the following breeding season. Intriguingly, annual berry consumption in December was not related to berry abundance, and individuals consuming more berries tended to have slightly lower return rates. Reproductive rate was not related to berry abundance. There was hardly support for a relation between immigration rates of first year breeders and berry abundance. Taken together these results imply that berry stock not only affected population size but also the population composition through sex specific exchange with the surroundings. Since population density covaried with berry abundance, density dependent effects provide an alternative explanation for the patterns observed.

Keywords: apparent survival, beech crop, population control, population density, sex, winter food

Introduction

A fascinating and important question in ecology is how populations are regulated (Lack 1954, Menge 2000, Sinclair 2003, Sibley et al. 2005, White 2008): bottom up, via the available resources, or top down by predators, parasites or diseases (Hunter 2001,

NORDIC SOCIETY OIKOS
www.avianbiology.org

Sinclair 2003). A first step to unravel the mechanism of population regulation is to estimate how population parameters like reproduction and survival covary with resources, and if so in what phase of the annual cycle. It is a challenge to quantify availability of the possible food types and the consumption rates by individuals, and subsequently translate these into demographic consequences.

Lack (1954) originally concluded that in bird populations food was an important limiting factor on the basis of rather general observations, i.e. 1) few adults appear to die from predation or disease, 2) birds are more numerous where food is more abundant, 3) different species living in the same region depend on different food supplies and 4) the occurrence of fighting for food. Subsequent work has quantified such aspects in more detail, and concludes that indeed food is an important factor limiting bird populations (Newton 1980, 1994) although different ideas exist about the importance of density dependence in this process (Krebs 2002, Sibley et al. 2005, White 2008).

Lack (1954) also suggested that population limitation, especially in non-migrating altricial birds, often occurs during the nonbreeding season, likely by mortality. In a study testing the generality of this idea in relation to climate factors, Sæther et al. (2004) concluded for altricial birds that most empirical work was consistent with an effect on population fluctuations outside the breeding season, in many cases through variation in survival rates (Cavé 1983, Møller 1989, Baillie and Peach 1992, Szép 1995, Barbraud and Weimerskirch 2001, Loison et al. 2002, Stokke et al. 2005). This supports the hypothesis of Lack (1954) that population limitation often occurs during the nonbreeding season.

Population abundance in and after winter in non-migrating songbirds has been shown to associate with winter food availability, and with winter survival rates (Lack 1954, Newton 1980). Specifically the relationship between the beech crop and the population dynamics of tit species has been well studied. Tit numbers are high after good beech crop (*Fagus sylvatica*) years, and lower after bad crop years, through associated variation in winter survival (Ulfstrand 1962, Perrins 1966, Balen 1980, Perdeck et al. 2000). Great tits eat beech mast frequently when available, suggesting a causal role for beech mast in explaining variation in tit population dynamics.

Experimental food supplementation in bird populations (Källander 1981, review by Newton 1994, Lahti et al. 1998, Perdeck et al. 2000, Cowley and Siriwardena 2005, Dhondt 2012) as well as in in mammal populations (Prevedello et al. 2013) shows that extra winter food positively affects population densities: winter food is often limiting. Moreover, in the Hoge Veluwe area (NL) the return rate of adult great tits only increased with food supplementation in low beech crop years, whereas in high beech crops years no experimental effect was observed, consistent with beech crop playing a causal role in mortality (Balen 1980, Perdeck et al. 2000).

But what do we know about the other natural winter foods used by the tit species? From the work of Gibb (1954) it is known (from direct observations) that great tits in the UK in winter not only forage on beech crop and hazelnuts but also on berries, next to a variety of insect food. Betts (1955) showed that from October to January a high proportion of great tits had nuts like acorn and hazelnuts besides beech crop in their stomachs. Ulfstrand (1962) claims that the tits in southern Sweden largely relied on beech mast for food in winters when it is abundant. So it seems not surprising that tit dynamics are associated with large scale estimates of beech crop production (Perrins 1966, Balen 1980, Perdeck et al. 2000). Although beech crop is likely causally involved, strict proof whether any natural winter food is causally involved in tit dynamics cannot be given because experiments manipulating the natural winter food abundance are lacking (see also Krebs et al. 2009 concerning rodents). Moreover, tit population dynamics covary with the beech crop index when seed producing beeches are locally absent, suggesting that there are other factors involved (Perrins 1966, Tinbergen et al. 1985, Perdeck et al. 2000, see also discussion Dhondt 2012).

Here we pursue the idea that tit population dynamics may be related to other winter food sources than beech crop. We know from the work of Snow and Snow (1988) that great tits do eat various kinds of berries and from our own work that they also do so in the Lauwersmeer population, living in an area reclaimed from the sea (Vollmer et al. 2007). Specifically we studied whether the dynamics of a local tit population was associated with the abundance of sea buckthorn berries *Hippophae rhamnoides*. Our study population is characterised by the fact that beech is absent from the study area and sea buckthorn berry bushes are amply available throughout the area. Sea buckthorn berries are eaten regularly by tits judged from direct observations and faeces produced in the roosting boxes. Over a period of six years we estimated berry abundance and an index of individual tit berry consumption that we related to 1) breeding population size, 2) sex- and age-specific winter disappearance until and after mid-winter, as well as 3) immigration rate and reproduction.

Methods

Study area

The Lauwersmeer study area (the Netherlands, 53°22′30″N, 6°11′55″E) was reclaimed from the Wadden Sea in 1968. Woodlands were planted, interspersed by grassy areas (Tinbergen 2005). Along the edges of the woodlands ample sea buckthorn bushes grow (Fig. 1). In the wooded areas a tit study population of both great and blue tits inhabited 12 plots with 50 nest boxes each (Nicolaus et al. 2012, Fokkema et al. 2016). During the winters of 2008/2009–2013/2014 data were collected on sea buckthorn berry production of a selected number of bushes in the central area and on the tit population roosting and breeding in nest boxes in winter and spring.

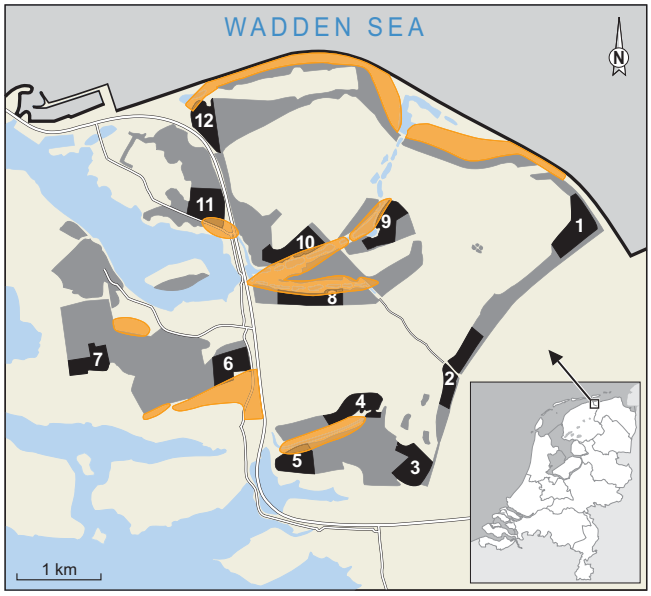

Figure 1. Map of the study area with the 12 study plots indicated in black. Each plot consisted of 50 nest boxes. Wood lots without nest boxes are dark grey. The inland light grey area represents the Lauwermeer Lake. The white areas are non-woody surroundings, mostly consisting of grass or agricultural land. The largest concentrations of buckthorn bushes were found in the orange areas. We quantified the buckthorn berry abundance in 19 bushes in the three buckthorn areas in the central area (plots 8, 9 and 10). Two villages are located near the north west corner of plot 11 and plot 7 respectively.

Standard program

In the breeding season weekly nest box checks allowed us to estimate basic breeding parameters of great and blue tits (for details see Tinbergen 2005, Fokkema et al. 2017). Great tits were ringed with a unique set of identification rings in the breeding season or in winter during roost checks to allow individual identification. Females were identified based on these identification rings when incubating, or, for both sexes, later at capture in the nest box with a spring trap when young were ca seven days old. If not yet ringed, parents were ringed with one metal ring (provided by the Dutch Bird Ringing Centre) and a unique combination of three plastic colour rings. Colour-rings of birds that were hard to catch (mainly males) were often read outside the breeding box using binoculars or a scope. The young were fitted with a metal ring when six days old and with colour-rings at day 14. Of the parents that produced a complete first clutch 95% of the females and 85% of the males were identified (failures of identification partly related to predation before identification; Fokkema et al. 2017). The ringing program was intensive and consistent over 1994–2015. In December, i.e. mid-winter, all nest boxes were checked at night for roosting tits. The number of breeding blue tits and their breeding success was registered as well, but blue tits were not individually marked.

Estimates of the breeding population

The female breeding population was estimated as the number of great or blue tits that laid a first egg during the period of 30 d after the first egg of that species was laid that year (defined as first broods). The tit species was determined on the basis of egg diameter (Fokkema et al. 2018) or when detected incubating the eggs. A number of nests was lost before the female was identified (on average 11.3%). Such females may produce a repeat clutch, and then be identified, others are lost. This leads to an overestimation of the breeding population. Because we lack the possibility to control for such unknown females in the blue tit since they were not ringed, we used the 'raw' number of first broods to estimate the breeding population for both blue and great tits, but also present the minimum number of breeding great tits as based on the individually know birds.

Estimates of the winter population

The winter population of great tits was estimated as the number of great tits that roosted in one of the 600 nest boxes during the roost checks in December. The tits were captured at night in their roosting box, the great tits identified if ringed, and ringed if needed as described before. About one fifth of the sleepers were blue tits (19.2%, n = 2585 sleepers), an underrepresentation of blue tits relative to the great tits as compared to the breeding season (44%, n = 2234 breeding pairs).

Return rate, recapture probability and apparent survival rate estimates

We used the sex- and age-specific return rate and recapture probability for all individually known great tits over different periods to estimate their annual apparent survival on the basis of recaptures within the study area.

Return rate was defined as the number of birds identified in period t + 1 divided by the number of identified birds in period t for each category. Return rate was estimated from the breeding season to mid-winter, from mid-winter to the next breeding season and from the breeding season to the next. Return rate estimates from the breeding season onward were made for known breeding females and males and for the locally born offspring that were known to have fledged from a first brood.

Not all great tits that used our nest boxes in the breeding season were identified. We define the sex-specific recapture probability as the probability that a marked bird, that is known to be alive from both earlier and later captures, is captured in the study area at a particular season (breeding season or at the mid-winter roost check) for the years 2007–2014. This was done because not all great tits that used our nest boxes in the breeding season were identified. Moreover natural holes may have been used for breeding and sleeping. In the Lauwersmeer area, a relatively young wood, the number of natural holes was low as judged from what

we detected during the nest box checks and also when we actively searched for them outside the nestbox plots in later years (Fokkema et al. 2018).

We estimated the apparent survival by dividing the return rate estimates (based on posterior parameter estimates of logistic regressions, Table 2a–c) by the mean recapture probability for the relevant sex, period and berry abundance (as calculated in the Supplementary material Appendix 3 Table A3, Fig. 4). The data points shown in Supplementary material Appendix 10 Fig. A10 are recapture rates corrected for the measured recapture probability for the period and the year of interest (data points in Fig. 4).

First-year birds are known to disperse more widely than adult birds, resulting in emigration from and immigration into the population. Of the 293 individuals that bred in two or more years not a single one switched between breeding plots (up to 6 km distance between plots, see map) suggesting low breeding dispersal. The return rate estimates from mid-winter to the next breeding season hardly differed between local and non-local birds (analysis not shown).

Sea buckthorn berry abundance

We used data of 19 sea buckthorn bushes in the central study area that were available all six years to estimate berry abundance (December 2008–2013). We estimated the number of berries per bush by estimating the number of berries per quantity of 100.

For 2009–2010 we miss data for five bushes, due to heavy snowfall making the counts in December impossible, but these missing counts were not the cause for the relatively slow decrease in berry numbers from November to December in that year (analysis not shown). We took the mean berry number per bush in December as an estimate of the abundance for that winter because we also had estimates from the berry consumption of the tits in that month. Results of analyses to be presented were similar when using the mean over all months or means of December and January.

Covariates of sea buckthorn abundance

Potential factors known to be involved in great tit population dynamics other than berry production are winter severity and population density (van Balen 1980, Perdeck et al. 2000). We checked whether these factors could also predict tit population dynamics in our population. For previous year breeding density the number of first broods in that breeding season was taken. For winter severity we used the Hellman number (KNMI: the number of days (24 h) with a mean temperature below 0°C between 1 November and 31 March including the winter of interest). Both measures were standardized as Z-values ((x − mean(x))/SD(x)). Beech crop is known to correlate with tit numbers and tit return rate in other populations (Van Balen 1980, Perdeck et al. 2000) but was not available in the Lauwersmeer. Yet, beech crop production as measured in the province of Drenthe (60 km distance, R. Bijlsma pers. comm., Kleef and Wijsman 2015) did covary with berry abundance in the Lauwersmeer (beta = 0.71, 89% HPDI: −0.10 to 1.47, for explanation HPDI see statistics).

Sea buckthorn consumption

From observations and photographs we know that the tits eat buckthorn berries. As far as we know great and blue tits are pulp eaters, holding a berry between their feet eating the flesh, probably discarding the seed. Tits often produced droppings while roosting in the nest box in winter. From these droppings we estimated an index of berry consumption, possible because the berries are bright orange and dye the faeces when eaten in sufficient numbers. There is a clear relation between the colour of the faeces and the number of berry skins that were found in the droppings while remains of seeds were never detected consistent with the impression that the great tits did not eat the seeds (Vollmer et al. 2007). Three categories of dropping scores were distinguished in the roosting box when a tit was found sleeping and had produced fresh droppings, i.e. 1) fresh dark droppings without any sign of berry consumption, 2) fresh intermediate coloured brownish droppings (with intermediate fraction of berry skins) and 3) fresh orange droppings (consisting of a high fraction of berry skins). If not disturbed, tits tend to roost in the same nest box on consecutive nights (Drent 1987, Fokkema et al. 2016) making it possible to assign fresh droppings to the individual bird sleeping in that box. These scores gave an index of individual berry consumption. For an index of the annual berry consumption we calculated the fraction of fresh orange droppings over all fresh droppings (n score 3/(n score 1 + n score 2 + n score 3)) in the December roost check. The data were collected for the years 2008–2013.

Artificial winter food

Throughout the study artificial winter food, provided by the general public, was available in two villages west of the study area (Fig. 1) and their feeders were used by great tits from our population. To facilitate other studies in the study area during two of the six winters, 2008/2009 and 2013/2014 we provided extra feeders at 12 different places throughout the study area during mid-winter. In 2008/2009 food was provided from August to February for one in four weeks to reduce the expected effect on return rate (Radersma 2011), while in 2013 food was provided continuously (Fokkema 2017).

Mixed model to estimate individual return rate from mid-winter to the next breeding season

We performed a multi-level analysis, including plot and year as random factors studying simultaneous variation on the year level (mean annual berry abundance and mean annual poop score (DDY)) and on the individual level (DDI) in terms of poop score relative to the annual mean poop score

and sex as explanatory variables to explain individual variation in return rate (van de Pol and Wright 2009).

Immigration

The ringing program allowed us to distinguish locally born birds from immigrants on the basis of their rings. All birds were sexed based on their plumage and assigned as first-year birds or older based on their wing coverts (Svensson 1992). First-year birds that were not born locally were called immigrants, adult birds were called locals when known to have bred in the study area in the previous year (thus including former immigrants), and non-locals if not. Because at the time of trapping the birds' sex was determined, sex-specific immigration rates could be calculated for the breeding season by dividing, per sex, the number of first-brood immigrants by the number of first-year known breeders.

Reproduction

To study associations between reproduction and berry availability we estimated the reproductive rate of the great tits. As estimates of the annual reproductive rate the annual mean number of chicks in the first brood and both the mean brood weight and mean chick weight when the nestlings were six days old were taken (to the tenth of a gram, first hatched chick = 0 d old). The twelve percent of nests that produced a first egg but failed before day six were not included in this estimate. We used the data when the nestlings were six days old because after that time point brood sizes were manipulated and subsequent breeding results were thus affected by us, in favour of other ongoing studies (Radersma et al. 2011, Fokkema et al. 2016, 2017).

Statistics

We fitted Bayesian Markov Chain Monte Carlo (MCMC) models with weakly informative priors (Supplementary material Appendix 1), using the packages BMRS (ver. 2.4.0), Rethinking 1.59 (McElreath 2016) and RStan 2.15.1 (Stan Development Team 2016) in R ver. 3.5.1 (R Development Team). We analyzed trends in the counts of berries with age using a negative binomial regression to account for over dispersion relative to a Poisson model (WAIC Poisson 288301, WAIC negative binomial 1567.4), a Gaussian regression model for the annual variation in the number of breeding pairs, while life history variables as return rate and recapture probability were analyzed using logistic binomial models. Year was introduced as a random factor in all models to estimate the between-year effects and when we needed to control for the repeated measures within years. As explanatory variables we used the annual mean number of berries per bush (standardized over the whole material) in December. In the multilevel binomial models where we used binary data of individual return rate (0 or 1) we simultaneously estimated effects of between-year and within-year (between individual) variation by adding year as a random factor in the analysis of individual variation in return rate. In this analysis we also added study plot (n = 12) as a random factor to control for variation between areas.

Models were compared with the widely applicable information criterion (WAIC) and WAIC-based weights. In the graphs and the tables we present means and spread of the dependent variable calculated on the basis of the posterior distributions of the parameter estimates. Maximum and minimum values of the parameter estimates as well as the grey areas in the graphs represent 89% HPDI intervals (highest posterior density interval which is the narrowest interval containing the specified probability mass (here 0.89)) of the value concerned. We used 89% HPDI, following the suggestion of McElreath (2016) to, when using a Bayesian approach, attend the reader to the fact that a HPDI differs from a 95% confidence interval as used under the hypothesis testing approach. We used the posterior probability distribution of the relevant parameter estimates to calculate the fixed effects of the independent parameters (berries, sex). Random effects were sub-sampled from the estimates for the years (n = 6) and the area (n = 12) to calculate the random effect adjusted intercept for each sample of the posterior.

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h31dh73> (Tinbergen et al. 2019).

Results

Sea buckthorn berry abundance

Sea buckthorn berry abundance differed between years, while within years the estimated mean number of berries per bush declined rapidly over the months (Fig. 2). There was no indication that the relative age of the bush did affect berry production measured in December (tested for 14 bushes of which we had data for 2008–2013, negative binomial

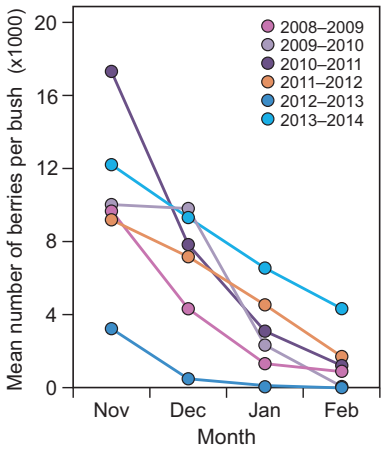

Figure 2. Mean number of berries per bush in the course of the winter season for the six study years.

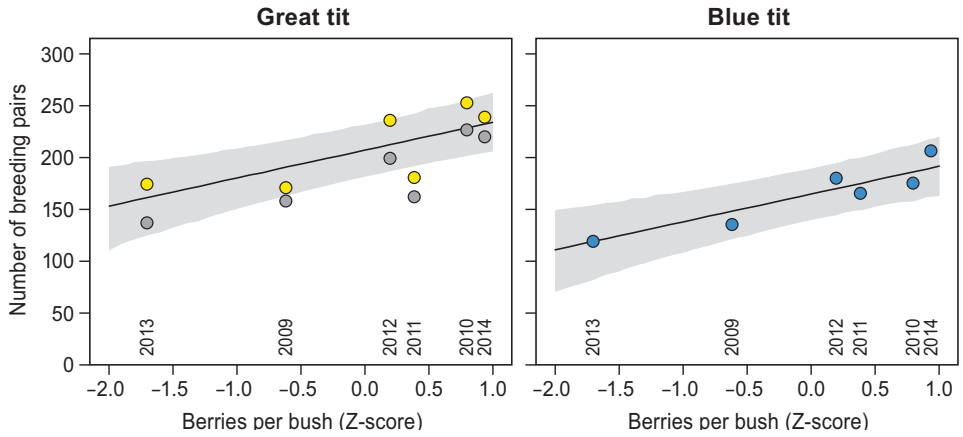

Figure 3. The number of breeding pairs as a function of the berries per bush (Z-score) for great and blue tits. Year indicates the year of breeding; the berries per bush were measured in the previous December. Lines are the means and grey areas the 89% HDPI intervals of the number of breeding pairs, calculated from the posterior distribution of the parameter estimates of model mss2 (Table 1). The grey points represent a minimum estimate of the number of great tits that started a breeding attempt based on individually known great tits. The coloured points represent a maximum estimate consisting of all tits that laid at least one egg and for which the species was known.

regression including year identity and bush identity as random factors explaining variation in berries per bush, trend over centred years (year −2 to 3), slope = −0.09, 89% HPDI: −0.79 to +0.59, Supplementary material Appendix 2 Table A2).

Number of breeding birds

On average 209 great tit (SD = 38, n = 6) and 163 blue tit pairs (SD = 32, n = 6) bred in the study area during 2009–2014. In the best supported model (Fig. 3, Table 1, model mss2) the number of breeding tits was positively associated with berry abundance in the previous December. There were on average 42 (89% HPDI: 25–59) more pairs of great tits than blue tits. A 1 SD increase in berry abundance resulted in an increase of 27 breeding pairs (89% HPDI: 11–42) in both species (i.e. around 15% of the mean breeding population) with little support for a different effect between the species (Table 1, model mss1).

The number, sex ratio and age of sleepers mid-winter

The total number of roosting great tits in mid-winter (Z-score) was negatively associated with the berry Z-score in the same winter (slope = −0.80, 89% HPDI: −1.45 to −0.10, n = 6). This was possibly due to the fact that breeding densities (Z-scores) tended to be relatively high in the years preceding a winter with low abundance of berries (slope = −0.67, 89% HPDI: −1.48 to 0.17, n = 6). Neither the fraction of roosting females (slope = −0.22, 89% HPDI: −1.26 to 0.85, n = 6) nor the fraction of young birds (slope = 0.38, 89% HPDI: −0.74 to 1.45, n = 6) was related to the berry Z-score (analysis not shown). On average 39 percent of the roosting birds were females (n = 2079). 54 percent of the females (n = 820) and 51 percent of the males (n = 1259) were first-year birds.

Recapture probability

The recapture probability was high (0.89, 89% HPDI: 0.86–0.91, n = 631). There was only slight support for the annual recapture probability to depend on berry abundance, and clear support for an interaction between sex and period (Fig. 4, Supplementary material Appendix 3 Table A3, model mrp3). The recapture probability for females was lower than for males during the roost checks mid-winter (all years 0.81 versus 0.91), but not in the breeding season (all years 0.93 versus 0.90).

Table 1. Gaussian models explaining variation in the number of breeding pairs on the basis of variation in the annual berry Z-score and the species (GT as reference species). Year was taken as a random effect. The model with most support (indicated with a star) includes both species and berry Z-score as explanatory variables, while the model with an interaction between berries and species was supported less.

	Random year	Intercept	Berriec	Species (P)	Species* berriec	Waic	Deltawaic	Weight
mss2*	1	1	1	1		108.62	0	0.6647
mss1	1	1	1	1	1	111.11	2.49	0.186
mss5	1	1		1		111.35	2.73	0.165
mss3	1	1	1			121.33	12.71	0.001
mss4	1	1				124.62	16	0
Estimates mss1	SD	intercept	beta	beta				
Mean	15.61	206.4	26.93	−42.17				
Lower 89% HPDI	1.98	189.81	11.25	−59.06				
Upper 89% HPDI	33.87	222.51	41.58	−24.16				

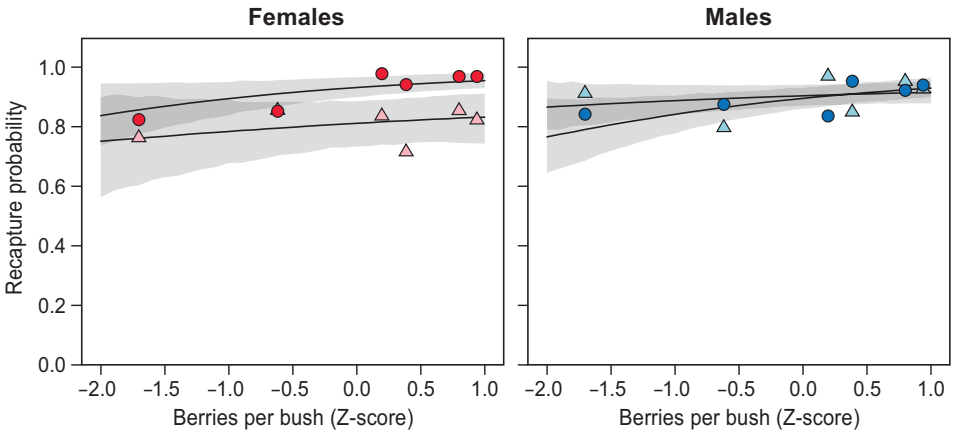

Figure 4. Logistic fit of the recapture probability (based on model mrp3, Supplementary material Appendix 3 Table A3) as explained by annual berry abundance (Z-score), sex (male = 1, female = 0) and season (spring = 1, winter = 0). Lines represent the means and grey areas the 89% HPDI intervals of the recapture probability calculated from the posterior distributions of the parameter estimates of model mrp3 for the different categories. Females: dark red summer, light red winter, males: dark blue summer, light blue winter.

Return rate over the non-breeding season

We found associations between the return rate and the berry abundance that differed between seasons (Fig. 5). Between breeding and mid-winter the overall return rate was not related to berry abundance in the same winter (beta +0.06, 89% HPDI: −0.15 to +0.28). Breeding males had higher return rates than breeding females (0.48 versus 0.30) and return rates of juveniles were much lower (0.09). The posterior mean for the berry effect was not very different from zero: +0.06, 89% HPDI: −0.15 to +0.28 indicating a weak berry effect (Table 2a model msw5, estimates not given in the table). The highest support of the model including the interaction between berries and age–sex groups (Fig. 5a, Table 2a, model msw1) is due to the fact that juvenile return rates tended to have a positive relationship with berry abundance (beta = 0.17), females tended to a negative (beta = −0.12) and males to have no relationship (beta = 0.0, Fig. 5a, Table 2a, model msw1).

In contrast to the period from breeding till mid-winter, in the period from mid-winter to the next breeding season return rate was positively associated with berry abundance for juveniles as well as males and females (the overall posterior distribution for the berry effect was (+0.72, 89% HPDI: 0.18–1.23) and differed between age and sex groups. Return rates of juveniles tended to be lower than return rates of the adult birds (Fig. 5b). The model combining age sex group and berry effects had considerable support (Table 2b, model mws2), underpinning a berry effect particularly in the second half of the winter (see Supplementary material Appendix 4 Fig. A4 for the posterior distributions of the slopes of the return rate with respect to berry abundance for respectively the first and the second half of the winter).

The return rate over the whole winter (from breeding season to breeding season) was roughly consistent with this picture. Juveniles had lower return rates than their parents but for all three categories of birds return rate was strongly positively associated with berry abundance (Fig. 5c, Table 2c, model mss1). The effect size was large: return rate for males almost tripled and for females and juveniles it doubled over the observed range of berry abundances. Moreover, the outcome of the analysis gives considerable support for the interpretation that the effect of berry abundance was sex-specific (the effect for males was steeper than for females, Table 2c, model mss1, posterior distribution of slope male – slope female: median = 0.251, 89% HPDI: −0.441 to −0.08). After low berry winters females were recaptured more often than males, but not after high berry winters.

Immigration

The proportion of immigrant first-year birds in the breeding population was 0.443 (89% HPDI: 0.364–0.527) and not clearly related to berry abundance in the previous winter (Fig. 6a). The data suggest that at high and low berry abundance relatively more settlement of young immigrant birds occurred for both sexes. Yet, simpler models including sex and berries or sex alone as explanatory variables had a similar support (Supplementary material Appendix 5 Table A5). More data are needed. For the adult birds, the fraction of birds that were not identified breeding in the previous year was low, and no clear pattern in relation to the berries existed (analysis not shown).

Annual variation in berry consumption

In contrast to our expectation annual berry consumption hardly varied with berry abundance. Judged from the faeces in the roosting boxes berry consumption in December was considerable in all years (a fraction of 0.42–0.77 of the birds had the highest score, Fig. 6b, Supplementary material Appendix 6 Table A6).

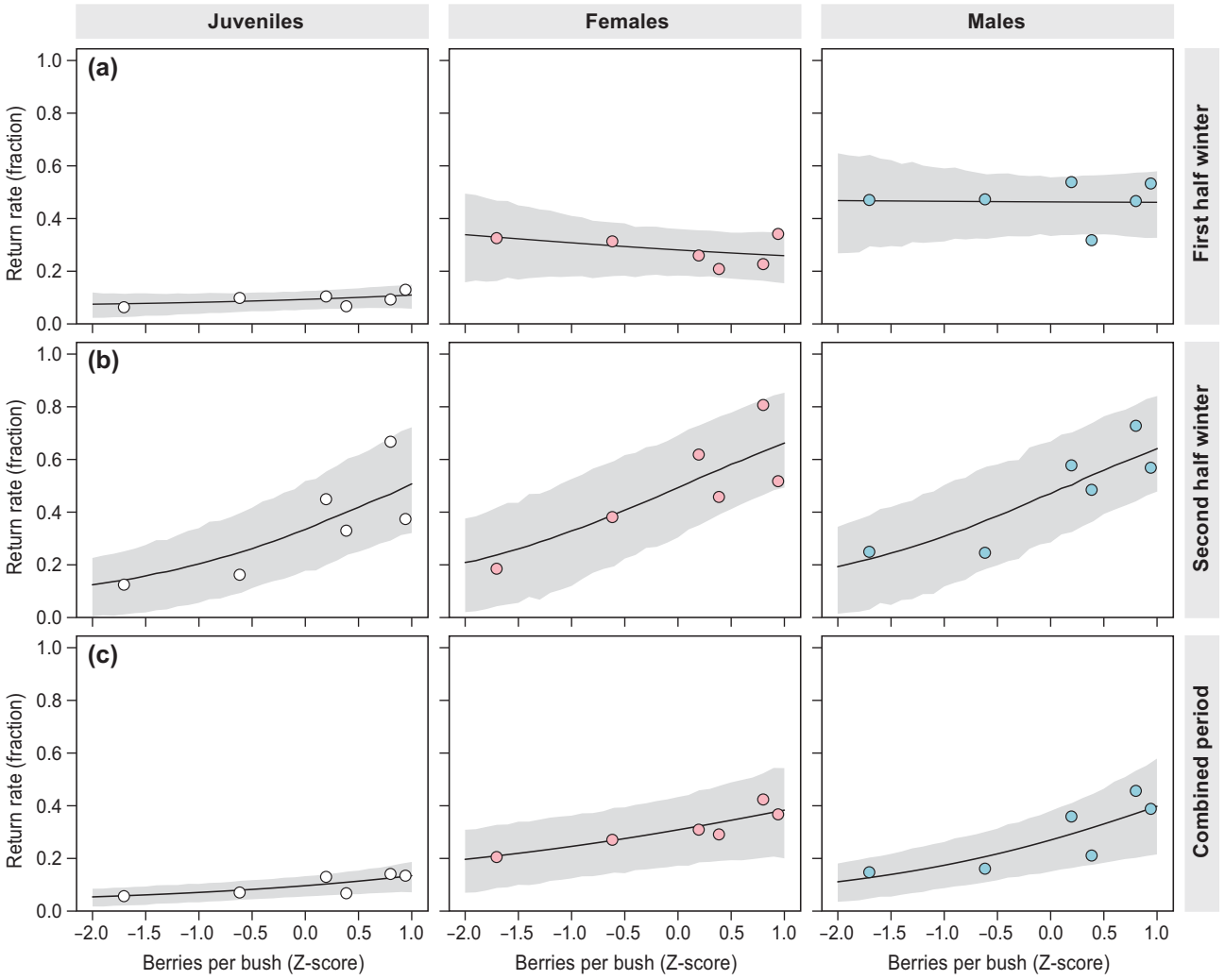

Figure 5. The return rate as a function of the berries per bush (Z-score) for first year juvenile, adult male and adult female great tits over: (a) the first half of the winter, (b) the second half of the winter and (c) the combined period. The berry abundance per bush was measured in December. Lines are the means, grey areas the 89% HPDI intervals of the return rate calculated from the posterior distribution of logistic models including the interaction between group and Z-score of the berries for each of the periods separately (Table 2a–c).

Individual return rate from December till the next breeding season

Both male and female return rate were associated with the annual berry abundance: more berries resulted in a higher annual return rate (Fig. 7a), consistent with our analysis discussed above concerning return rate from breeding season to breeding season. To our surprise the index of berry consumption, both between years and within years, predicted rather a negative effect of berry consumption on return rate: the higher the berry consumption the lower the return rate (Fig. 7b–c, Supplementary material Appendix 7 Table A7). Although the model without the index of berry consumption estimates also has considerable support (Supplementary material Appendix 7 Table A7, model m7), the outcome does suggest, against our expectation, a negative relation between berry consumption and return rate, rather than the expected positive relationship.

Reproductive rate in relation to berry production

From the breeding attempts that started in our nestboxes 12% (89% HPDI: 7–19%) failed before day six, and failure was only weakly dependent on the berry abundance in the preceding winter (slope = –0.34, 89% HPDI: −1.37 to 0.71, see also Fig. 3 left panel, compare minimal with maximal number of breeding birds). Few unringed individuals were spotted during the breeding season, suggesting that a high proportion of breeders used our boxes. Successful first broods, measured in the boxes when the oldest nestling in the brood was six days old, produced on average 7.64 (SD 1.78) nestlings annually with mean individual weight of 8.40 g, leading to an overall mean brood weight of 64.38 g. There was no support for an association between annual values of these three parameters of reproduction and the berry Z-score in the previous winter, nor in the following winter (Supplementary material Appendix 8 Table A8).

Table 2. Comparison of the WAIC and the weight of a number of logistic models explaining the return rate of great tits in relation to the annual berry Z-score, the age–sex groups (juveniles as the reference category) and the interaction between berry Z-score and the age–sex groups for three time periods: (a) the first half of the winter (breeding season till December), (b) the second half of the winter (December till the next breeding season) and (c) the whole winter (breeding season till next breeding season). Year was taken as a random effect. The estimates of the model chosen (indicated with a star) with their 89% HPDI intervals are given in the table with the factors.

	Random year	Intercept	Berriec	Female	Male	Female* berriec	Male* berriec	Waic	Deltawaic	Weight
(a) In the first half of the winter the full model including both age–sex groups, berry Z-score and their interaction as explanatory factors has most support (Fig. 5a)										
msw1*	1	1	1	1	1	1	1	129.12	0	0.998
msw3	1	1		1	1			143.43	14.31	0.001
msw2	1	1	1	1	1			143.62	14.50	0.001
msw4	1	1						1303.2	1174.08	0
msw5	1	1	1					1312.5	1183.38	0
Estimates msw1	SD	intercept	beta	beta	beta	beta	beta			
Mean	0.41	−2.31	0.17	1.35	2.15	−0.29	−0.17			
Lower 89% HPDI	0.18	−2.62	−0.15	1.22	2.02	−0.43	−0.31			
Upper 89% HPDI	0.81	−2.03	0.52	1.48	2.27	−0.15	0.04			
(b) In the second half of the winter the model including age–sex and the model including age–sex and berries had similar support. We give the parameter estimates for the second best model (*) because we are interested in the effect of the berry Z-score on the return rate (Fig. 5b)										
mws3	1	1		1	1			101.07	0	0.49
mws2*	1	1	1	1	1			101.23	0.16	0.46
mws1	1	1	1	1	1	1	1	105.61	4.54	0.05
mws4	1	1						138.67	37.60	0
mws5	1	1			1			138.91	37.84	0
Estimates mss2	SD	intercept	beta	beta	beta					1
Mean	0.77	−0.74	0.75	0.70	0.61					
Lower 89% HPDI	0.33	−1.28	0.19	0.45	0.38					
Upper 89% HPDI	1.59	−0.2	1.32	0.95	0.83					
(c) Over the whole period, from breeding season to breeding season the full model including both age–sex groups, berry Z-score and their interaction as explanatory factors has most support (Fig. 5c)										
mss1*	1	1	1	1	1	1	1	132.41	0	0.733
mss3	1	1		1	1			135.81	3.40	0.134
mss2	1	1	1	1	1			135.82	3.41	0.133
mss4	1	1	1					731.00	598.59	0
mss5	1	1	1					732.74	600.33	0
Estimates mss1	SD	intercept	beta	beta	beta	beta	beta			1
Mean	0.42	−2.25	0.37	1.44	1.25	−0.03	0.22			
Lower 89% HPDI	0.18	−2.54	0.05	1.32	1.11	−0.18	0.06			
Upper 89% HPDI	0.88	−1.97	0.68	1.57	1.39	0.12	0.39			

Covariates of berry production

There was no support for an association between berry abundance and winter severity (slope = −0.10, 89% HPDI: −1.16 to 1.01). In the study years preceding winters with low berry abundance, tit densities were high, potentially explaining the lower return rate in these years through negative density dependence instead of positive berry effects (association between tit density in the preceding winter and berry abundance slope = −0.67, 89% HPDI: −1.48 to 0.17). We therefore repeated the return rate analysis (breeding to breeding) including berry abundance, winter severity and breeding density as explanatory variables. Winter severity did not explain variation in return rates (slope = −0.04, 89% HPDI: −0.24 to +0.15), perhaps because the winters in this period were mild to normal. Breeding density, however, was, as explanatory variable, exchangeable with berry abundance, and had even more support than the berry model (Supplementary material Appendix 9 Table A9: model mss3). The second highest ranking model included both berry abundance and population density where the sex–age category interacted with population density, not with berry abundance. This model produces apart from density effects also an estimate for the effect of berry abundance: slope = 0.21, 89% HPDI: −0.07 to 0.51.

Discussion

A large fraction of the great tits in the Lauwersmeer population consumed sea buckthorn berries in all winters. The numbers of breeding pairs of both great and blue tits were positively related to the winter berry abundance in the previous December. Consistent with this, great tit return rate from breeding to breeding was positively related to berry abundance. The berry abundance related disappearance took place in the second half of the winter and over the whole winter differed between the sexes.

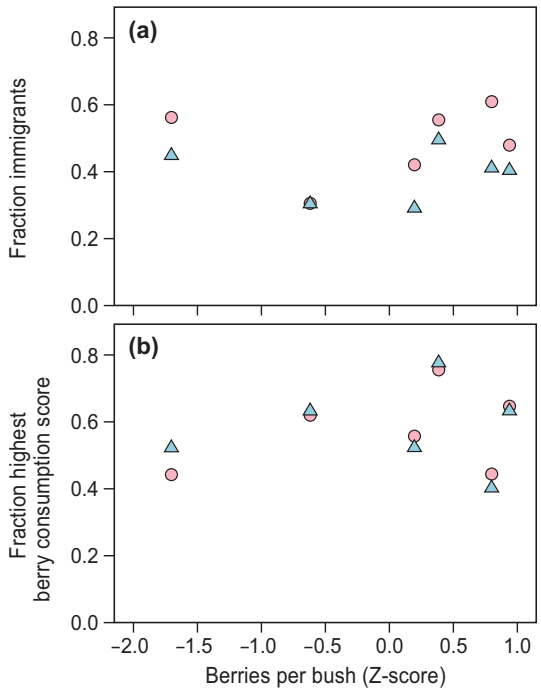

Figure 6. (a) The annual fraction of first year birds that immigrated in the breeding population as a function of the berry abundance per bush (Z-score) in the previous winter, plotted for females (pink) and males (light blue). (b) The annual fraction of individuals with the highest score of berry consumption based on the coloration of their feces (score 3/(score 1 + score 2 + score3)) as a function of the mean number of berries per bush (Z-score) both measured in December, plotted for females (pink) and males (light blue).

Recapture probability was high and not strongly related to berry abundance (Supplementary material Appendix 3, Fig. 4) meaning that the conclusions regarding return rate also apply to the apparent survival rate (Supplementary material Appendix 10 Fig. A10). Sea buckthorn berries are thus a candidate to control local great tit populations bottom up.

These findings are in line with our earlier results (Vollmer et al. 2007) where we detected positive associations between tit diet, roosting box occupation rate, local immigration rate and berry abundance. The latter patterns were based on spatial variation in berry abundance within a year rather than temporal variation between years as analysed in the current study.

In the current study the winters that we provided extra food (2008/2009 and 2013/2014) also happened to be winters with lower berry abundance. Potentially the impact of low berry abundance may have been more severe, but we have no way to estimate this.

The decline in great tit numbers took place in the second half of the winter, also the period of the year that berry abundance clearly diminished. That berry abundance in December was not yet limiting is consistent with the fact that berry consumption, based on the faeces measurements, in December was still high in all years concerned, even though the abundance of berries on offer varied a lot between years (Fig. 2). Apparently the tits could still exploit the berries successfully during December. In a later phase of the winter, the dwindling berry abundance, in concert with the presumable decline in available insect food, may indeed have caused food shortage and subsequently berry-related mortality. The late winter disappearance of the tits is consistent with the finding of Nicolaus et al. (2012) in the same population. In their study experimentally induced effects of local offspring sex ratio on great tit return rate, which was probably mediated by competition, also took place in the second half of the winter. Unfortunately we did not collect faeces estimates later in winter, the likely critical period, and thus could not test the relationship between tit return rate and berry consumption further.

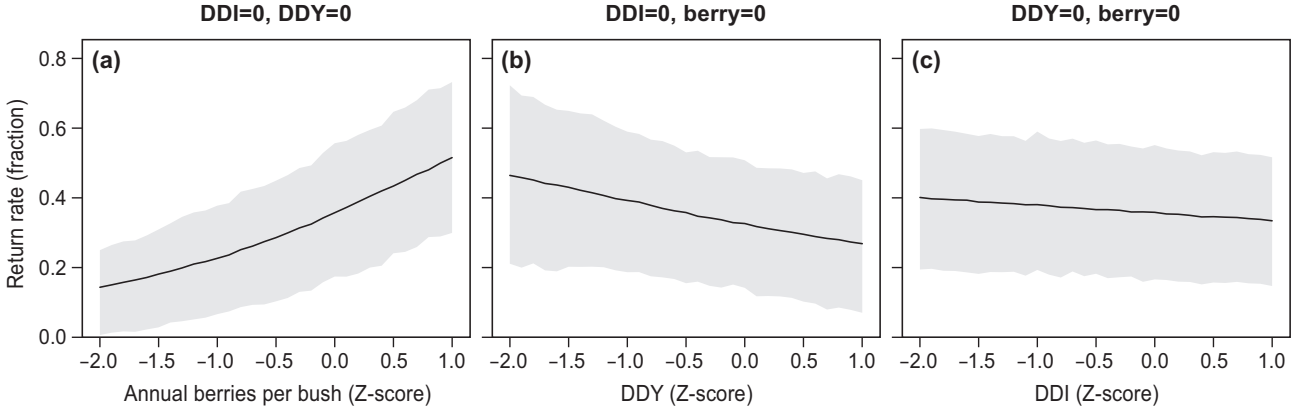

Figure 7. The marginal effects of (a) annual berry production, (b) annual mean buckthorn berry consumption score (DDY) and (c) individual buckthorn berry consumption score DDI (all Z-scores) on return rate. Lines are means and grey areas 89% HPDI intervals calculated from the posterior distribution of parameter estimates (based on logistic model m5 for females, Supplementary material Appendix 7 Table A7). Consistent with the earlier results there was (a) a positive relation between local recapture rate and annual berry Z-score. In contrast there is some support for a negative relation between survival and berry consumption score on both (b) the annual level and (c) the individual level. Birds that eat relatively more berries were less likely to return.

In the past, covariation between beech crop and weather led Perrins (1980) and White (1984) to formulate the breeding season food limitation hypothesis (Perdeck et al. 2000), suggesting that breeding success was related to the winter seed production to come (but see White 2007). Perdeck et al. (2000) found little support for this idea, and neither do we in the Lauwersmeer: there was no correlation between reproductive parameters and previous or subsequent berry production (Supplementary material Appendix 9). We conclude that winter survival and or dispersal of great tits are the parameters that covary with the berry abundance and not the reproductive rate.

On the basis of the differences in return rate between years and between individual birds within years we found evidence that, against our expectation, more berries in the faeces produced by roosting birds (here used as a measure of individual berry consumption) in December predicted rather a lower than a higher return rate in the next breeding season. Although the evidence is not strong, the negative tendency is evident both between and within years. The story is thus not simply the more berries the better! Perhaps a tit can also eat too many berries. A varied diet may be a better choice for various reasons. Perhaps the berries contain toxins (Levey and Cipollini 1998, Barnett et al. 2012, Oudman et al. 2014), or the berries are not a balanced food in terms of ingredients (Witmer 1998, 2001) or feeding on berries may be risky in terms of predation (Quinn and Cresswell 2004). Alternatively, diet may negatively covary with other bird (or year) qualities. Perhaps some birds are less well able to collect alternative food relative to others, and therefore eat a lot of berries. Such individuals may have a lower survival, not due to the berry consumption, but because of other correlated traits that set them apart. To find answers on all these questions we should start collecting better estimates of the diet throughout the winter with adequate availability estimates. In addition lab trials similar to those in frugivorous birds (Witmer 1998) and waders (Oudman et al. 2014) could give answers. Can the birds survive on pure berry diets? Are the berries important for winter fattening (Hernández 2009, Hertel et al. 2018)? In a pilot to exploit the possibilities for an experimental approach of this problem we offered great tits belonging to an inland population branches full with sea buckthorn berries in December on their feeding table outside. Although they did encounter the berries, the tits did not consume them at all! They preferred their normal feeding table food. This raises interesting new questions on habituation and social learning in food exploitation as relevant factors determining the way the birds value food.

Fewer females stayed in the Lauwersmeer area in winter, as judged from their relative low recapture probability in winter, from their lower occurrence in roosting boxes as well as in foraging areas in winter (unpublished observations). Females seem less affected by berry abundance. In years with low berry abundance females do better, while in years with high berry abundance this difference does not exist.

An alternative explanation for the observed patterns was that the population dynamic patterns was not related to berry production but to the previous seasons' breeding density (Supplementary material Appendix 9 Table A9). This model fits the data best and provides the posterior parameter estimates with the narrowest 89% HPDI intervals. Male return rate would then be stronger negatively related to breeding density than female return rate, while both sexes may profit from a higher berry abundance (Supplementary material Appendix 9 Table A9: model mss5, mss3 and mss1).

Because berry abundance and density covary in this relatively small dataset, interpretation of the separate estimates of density and berry effects have to be judged with caution due to potential collinearity. But the estimates suggest that the combination of effects of breeding density (−) and berry production (+) on the return rate could be involved in the case that there is competition for berries in the second half of the winter. Potentially this might be a causal chain, high breeding density might cause low berry abundance and subsequently reduce tit survival. At the moment we do not believe that this is the case because 1) the berry supply halfway the winter is enormous as compared to potential tit consumption 2) the number of the sleepers in December did not associate with berry decline from December to January (Z-scores: slope = −0.30, 89% HPDI: −1.32 to 0.75), 3) many other birds like thrushes (*Turdus iliacus*, *Turdus pilaris*) and starlings (*Sturnus vulgaris*) consumed the berries and 4) frost affects the berry abundance.

The fact that adult recapture rate varied in a sex specific way with berry abundance or density suggests potentially important ecological relationships. It implies sex specific influx and efflux of birds from the local population in association with berry abundance or density. Our data become too sparse to allow further splitting in the necessary categories. From other studies density effects are known to explain variation in different aspects of tit population dynamics (Tinbergen et al. 1985, Both and Visser 2000, Matthysen 2005, Wilkin et al. 2006, Nicolaus et al. 2013, Gamelon et al. 2016), and the sex specificity of these density effects is an interesting aspect for future studies to explore.

In general many alternative hypotheses for the beech crop (or buckthorn berry) related tit survival and dispersal exist. Because in any population various causal factors may act simultaneously or intermittently, always or sometimes, the question as to what factors are when and to what extent causally involved in tit survival and dispersal seems – in our opinion – near unsolvable. It needs experiments changing all factors independently to detect their causal role in the regulation of tit numbers (see also Krebs et al. 2009 discussing berry effects on small rodents).

That berries may have great ecological importance in general is illustrated by Ripple et al. (2014) in North America. They showed results from Yellowstone Park that are consistent with the idea of a trophic cascade involving berry production. Increased predation by wolves and other large carnivores reduced and redistributed the elk population,

decreased herbivory on berry producing shrubs and increased production of plant-based foods which in turn aided grizzly bears. We only studied one step of a what might have been a trophic cascade in the past, yet pointing at interesting aspects that may be important in other systems.

So what did we learn from this tit study in more general terms?

1) There is ample experimental evidence that winter food is important for tit population dynamics, yet our knowledge of winter diets of tits has not increased substantially since the work of Gibb (1954), Betts (1955) and Ulfstrand (1962). Consequently, the causal role of different natural foods in tit dynamics remains uncertain.

2) Our great tit population had no access to beech crop and used sea buckthorn berries as a winter food. Population dynamics in this population was positively related to annual berry crops and/or previous season's breeding density.

3) The observed patterns in tit dynamics in relation to the berry crop or population density were largely related to apparent survival or dispersal and not to patterns in reproductive rates, suggesting a bottom up effect of berries or density on tit population dynamics.

4) In contrast to the positive association between tit survival and berry abundance, the association between tit survival and berry consumption estimates tended to be negative, suggesting that more berries is not always better.

5) Since sea buckthorn berries occur in coastal and alpine areas, our findings may have implications for populations of tits and other birds living in such regions. But also in non-coastal populations tits may exploit different types of berries and we do not know the importance in those habitats. Berries, if available throughout winter, may be as important to great tit populations as beech crop.

6) That the sexes differ in apparent survival in relation to annual berry abundance and/or density is a point of general interest (and not really analysed in other studies). Differential mortality between the sexes will lead to differential exchange between the populations and their surroundings. Sex-specific effects of berry abundance and/or density on individual apparent survival can thus be considered a potential force in microevolution.

Acknowledgements – We thank the State Forestry Service 'Staatsbosbeheer' and the Royal Netherlands Army 'Koninklijke Landmacht' for letting us work in the Lauwersmeer area and for the opportunity to stay at the 'Willem Lodewijk van Nassau Kazerne'. We thank the master students and the students from animal ecology courses for their help in gathering breeding data and many colleagues for help in collecting the winter roosting data. C. Both, R. Bijlsma and M. Nicolaus were important in discussion and improved the manuscript substantially. Two anonymous reviewers greatly improved the manuscript.

Funding – The work was financially supported by the Netherlands Organization for Scientific research (NWO grant to JMT; grant number: 82201011, NWO Vici grant to JK 86503003) and the Groningen Univ.

Author contributions – JT wrote the paper and JT, RU and RWF collected data on the birds while RU and RWF were of prime importance to collect the data on the sea buckthorn berries, IP was of essential help to JT in applying the Bayesian statistics.

Permits – Permission for the work was given by the Groningen Univ. Animal Experiments Committee (Dec project 5548).

References

Baillie, S. R. and Peach, W. J. 1992. Population limitation in Palaearctic-African migrant passerines. – Ibis 134: 120–132.

Balen, J. H. van 1980. Population fluctuations of the great tit and feeding conditions in winter. – Ardea 68: 143–164.

Barbraud, C. and Weimerskirch, H. 2001. Emperor penguins and climate change. – Nature 411: 183–186.

Barnett, C. A., Skelhorn, J., Bateson, M. and Rowe, C. 2012. Educated predators make strategic decisions to eat defended prey according to their toxin content. – Behav. Ecol. 23: 418–424.

Betts, M. 1955. The food of titmice in Oak Woodland. – J. Anim. Ecol. 24: 282–323.

Both, C. and Visser, M. E. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. – J. Anim. Ecol. 69: 1021–1030.

Cavé, A. J. 1983. Purple heron survival and drought in tropical west Africa. – Ardea 71: 217–224.

Cowley, E. and Siriwardena, G. M. 2005. Long-term variation in survival rates of sand martins *Riparia riparia*: dependence on breeding and wintering ground weather, age and sex and their population consequences. – Bird Study 52: 237–251.

Dhondt, A. 2012. Interspecific competition in birds. – Oxford Univ. Press.

Drent, P. J. 1987. The importance of nestboxes for territory settlement, survival and density of the great tit. – Ardea 75: 59–71.

Fokkema, R. W. 2017. Family planning under social competition. – PhD thesis, Univ. of Groningen.

Fokkema, R. W., Ubels, R. and Tinbergen, J. M. 2016. Great tits trade off future competitive advantage for current reproduction. – Behav. Ecol. 27: 1656–1664.

Fokkema, R. W., Ubels, R. and Tinbergen, J. M. 2017. Is parental competitive ability in winter negatively affected by previous springs' family size? – Ecol. Evol. 7: 1410–1420.

Fokkema, R. W., Ubels, R. and Tinbergen, J. M. 2018. Experimentally quantifying the effect of nest-site depth on the predation risk and breeding success of blue tits. – Auk 135: 919–932.

Gamelon, M., Grøtan, V., Engen, S., Bjørkvoll, E., Visser, M. E. and Sæther, B. E. 2016. Density dependence in an age-structured population of great tits: identifying the critical age classes. – Ecology 97: 2479–2490.

Gibb, J. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. – Ibis 96: 513–543.

Hernández, Á. 2009. Summer–autumn feeding ecology of pied flycatchers *Ficedula hypolueca* and spotted flycatchers *Muscicapa striata*: the importance of frugivory in a stopover area in northwest Iberia. – Bird Conserv. Int. 19: 224–238.

Hertel, A. G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J. E. and Zedrosser, A. 2018. Berry production drives bottom–up effects on body mass and reproductive success in an omnivore. – Oikos 127: 197–207.

Hunter, M. D. 2001. Multiple approaches to estimating the relative importance of top–down and bottom–up forces on insect populations: experiments, life tables and time-series analysis. – Basic Appl. Ecol. 2: 295–309.
Källander, H. 1981. The effects of provision of food in winter on a population of the great tit *Parus major* and the blue tit *Parus caeruleus*. – Oikos 12: 244–248.
Kleef, H. L. and Wijsman, H. J. W. 2015. Mast, mice and pine marten (*Martes martes*): the pine marten's reproductive response to wood mouse (*Apodemus sylvaticus*) fluctuations in the Netherlands. – Lutra 58: 23–33.
Krebs, C. J. 2002. Two complementary paradigms for analyzing population dynamics. – Phil. Trans. R. Soc. B 357: 1211–1219.
Krebs, C. J., Cowcill, K., Boonstra, R. and Kenney, A. J. 2009. Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? – J. Mammal. 81: 500–509.
Lack, D. 1954. The natural regulation of animal numbers. – Oxford Univ. Press.
Lahti, K., Orell, M., Rytkonen, S. and Koivula, K. 1998. Time and food dependence in willow tit winter survival. – Ecology 79: 2904–2916.
Levey, D. J. and Cipollini, M. L. 1998. A glycoalkaloid in ripe fruit deters consumption by cedar waxwings. – Auk 115: 359–367.
Loison, A., Sæther, B. E., Jerstad, K. and Rostad, O. W. 2002. Disentangling the sources of variation in the survival of the European dipper. – J. Appl. Stat. 29: 289–304.
Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. – Ecography 28: 403–416.
McElreath 2016. Statistical rethinking, a Bayesian course with examples in R and Stan. – Chapman and Hall.
Menge, B. A. 2000. Top–down and bottom–up community regulation in marine rocky intertidal habitats. – J. Exp. Mar. Biol. Ecol. 250: 257–289.
Møller, A. P. 1989. Population dynamics of a declining swallow *Hirundo rustica* population. – J. Anim. Ecol. 58: 1051–1063.
Newton, I. 1980. The role of food in limiting bird numbers. – Ardea 68: 11–30.
Newton, I. 1994. The first Alfred Newton lecture presented at the 'Bird Conservation in Action' conference, April 1994: experiments on the limitation of bird breeding densities: a review. – Ibis 136: 397–411.
Nicolaus, M., Michler, S. P. M., Jalvingh, K. M., Ubels, R., van der Velde, M., Komdeur, J., Both, C. and Tinbergen, J. M. 2012. Social environment affects juvenile dispersal in great tits (*Parus major*). – J. Anim. Ecol. 81: 827–837.
Nicolaus, M., Brommer, J. E., Ubels, R., Tinbergen, J. M. and Dingemanse, N. J. 2013. Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird. – J. Evol. Biol. 26: 2031–2043.
Oudman, T., Onrust, J., de Fouw, J., Spaans, B., Piersma, T. and van Gils, J. A. 2014. Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate. – Am. Nat. 183: 650–659.
Perdeck, A. C., Visser, M. E. and van Balen, J. H. 2000. Great tit *Parus major* survival, and the beech-crop cycle. – Ardea 88: 99–108.
Perrins, C. M. 1966. The effect of beech crops on great tit populations and movements. – Br. Birds 59: 419–432.
Perrins, C. M. 1980. Survival of young great tits, *Parus major*. – Int. Ornithol. Congr. 17: 159–174.
Prevedello, J. A., Dickman, C. R., Vieira, M. V. and Vieira, E. M. 2013. Population responses of small mammals to food supply and predators: a global meta-analysis. – J. Anim. Ecol. 82: 927–936.
Quinn, J. L. and Cresswell, W. 2004. Predator hunting behaviour and prey vulnerability. – J. Anim. Ecol. 73: 143–154.
Radersma, R. 2011. The ecological and evolutionary consequences of brood sex ratio variation. – PhD thesis, Univ. of Groningen.
Radersma, R., Tinbergen, J. M. and Komdeur, J. 2011. Do brood sex ratio, nestling development and sex affect fledging timing and order? An experimental study on great tits. – Anim. Behav. 81: 69–75.
Ripple, W. J., Beschta, R. L., Fortin, J. K. and Robbins, C. T. 2014. Trophic cascades from wolves to grizzly bears in Yellowstone. – J. Anim. Ecol. 83: 223–233.
Sæther, B., Sutherland, W. J. and Engen, S. 2004. Climate influences on avian population dynamics. – Adv. Ecol. Res. 35: 185–209.
Sibley, R. M., Barker, D., Denham, M. C., Hone, J. and Pagel, M. 2005. On the regulation of populations of mammals, birds, fish and insects. – Science 309: 607–610.
Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. – Phil. Trans. R. Soc. B 358: 1729–1740.
Snow, B. and Snow, D. 1988. Birds and berries: a study of an ecological interaction. – T & A D Poyser.
Stan Development Team 2016. Stan: a C++ library for probability sampling. – Ver. 2.10.0.
Stokke, B. G., Møller, A. P., Sæther, B. and Rheinwald, G. 2005. Weather in the breeding area and during migration affects the demography of a small long-distance passerine migrant. – Auk 122: 637–647.
Svensson, L. 1992. Identification guide to European passerines. – British Trust for Ornithology.
Szép, T. 1995. Relationship between west-African rainfall and the survival of central-European sand martins *Riparia riparia*. – Ibis 137: 162–168.
Tinbergen, J. M. 2005. Biased estimates of fitness consequences of brood size manipulation through correlated effects on natal dispersal. – J. Anim. Ecol. 74: 1112–1120.
Tinbergen, J. M., Van Balen, J. H. and Van Eck, H. M. 1985. Density dependent survival in an isolated great tit population: Kluyvers data reanalysed. – Ardea 73: 38–48.
Tinbergen, J. M., Fokkema, R. W., Pen, I. and Ubels, R. 2019. Data from: sea buckthorn berries *Hippophae rhamnoides* L. predict size and composition of a great tit population *Parus major* L. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.h31dh73>.
Ulfstrand, S. 1962. On the nonbreeding ecology and migratory movements of the great tit (*Parus major*) and the blue tit (*Parus caeruleus*) in southern Sweden, with notes on related species. – Vår Fågelvärld 3: 1–145.
van de Pol, M. and Wright, J. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. – Anim. Behav. 77: 753–758.
Vollmer, A., Both, C. and Tinbergen, J. 2007. Duindoornbessen als wintervoedsel van de Koolmees. – Limosa 80: 68–75.
White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen stressed food plants. – Oecologia 63: 90–105.
White, T. C. R. 2007. Mast seeding and mammal breeding: can a bonanza food supply be anticipated? – N. Z. J. Zool. 34: 179–183.

White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. – Biol. Rev. 83: 227–248.
Wilkin, T. A., Garant, D., Gosler, A. G. and Sheldon, B. C. 2006. Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques. – J. Anim. Ecol. 75: 604–615.

Supplementary material (available online as Appendix jav-02037 at <www.avianbiology.org/appendix/jav-02037>). Appendix 1–10.

Witmer, M. C. 1998. Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. – Physiol. Zool. 71: 599–610.
Witmer, M. C. 2001. Nutritional interactions and fruit removal: cedar waxwing consumption of *Viburnum opulus* fruits in spring. – Ecology 82: 3120–3130.